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REVIEW

Connecting research and practice to enhance the evolutionary potential of species under climate change

Laura M. Thompson[1] | **Lindsey L. Thurman**[2] | **Carly N. Cook**[3] | **Erik A. Beever**[4] | **Carla M. Sgrò**[3] | **Andrew Battles**[5] | **Carlos A. Botero**[6] | **John E. Gross**[7] | **Kimberly R. Hall**[8] | **Andrew P. Hendry**[9] | **Ary A. Hoffmann**[10] | **Christopher Hoving**[11] | **Olivia E. LeDee**[12] | **Claudia Mengelt**[13] | **Adrienne B. Nicotra**[14] | **Robyn A. Niver**[15] | **Felipe Pérez-Jvostov**[16] | **Rebecca M. Quiñones**[17] | **Gregor W. Schuurman**[7] | **Michael K. Schwartz**[18] | **Jennifer Szymanski**[19] | **Andrew Whiteley**[20]

[1]U.S. Geological Survey (USGS), National Climate Adaptation Science Center and the University of Tennessee, Knoxville, Tennessee, USA
[2]USGS, Northwest Climate Adaptation Science Center, Corvallis, Oregon, USA
[3]School of Biological Sciences, Monash University, Melbourne, Australia
[4]USGS, Northern Rocky Mountain Science Center and Montana State University, Bozeman, Montana, USA
[5]Teladoc Health, Denver, Colorado, USA
[6]Washington University in St. Louis, St. Louis, Missouri, USA
[7]National Park Service (NPS) Climate Change Response Program, Fort Collins, Colorado, USA
[8]The Nature Conservancy, Lansing, Michigan, USA
[9]McGill University, Montréal, Canada
[10]University of Melbourne, Melbourne, Australia
[11]Michigan Department of Natural Resources, Lansing, Michigan, USA
[12]USGS, Midwest Climate Adaptation Science Center, Saint Paul, Minnesota, USA
[13]USGS, Land Management Research Program, Sacramento, CA, USA
[14]Australian National University, Canberra, Australia
[15]U.S. Fish and Wildlife Service (USFWS), Branch of Listing and Policy Support, Bailey's Crossroads, Virginia, USA
[16]Digital Research Alliance of Canada, Toronto, Canada
[17]Massachusetts Division of Fisheries and Wildlife, Westborough, Massachusetts, USA
[18]U.S. Forest Service, National Genomics Center for Wildlife and Fish Conservation, Missoula, Montana, USA
[19]USFWS, Branch of SSA Science Support, Division of Endangered Species, Onalaska, Wisconsin, USA
[20]University of Montana, Missoula, Montana, USA

Correspondence
Laura M. Thompson, U.S. Geological Survey (USGS), National Climate Adaptation Science Center and the University of Tennessee, Knoxville, TN, USA.
Email: lthompson@usgs.gov

Abstract

Resource managers have rarely accounted for evolutionary dynamics in the design or implementation of climate change adaptation strategies. We brought the research and management communities together to identify challenges and

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opportunities for applying evidence from evolutionary science to support on-the-ground actions intended to enhance species' evolutionary potential. We amalgamated input from natural-resource practitioners and interdisciplinary scientists to identify information needs, current knowledge that can fill those needs, and future avenues for research. Three focal areas that can guide engagement include: (1) recognizing when to act, (2) understanding the feasibility of assessing evolutionary potential, and (3) identifying best management practices. Although researchers commonly propose using molecular methods to estimate genetic diversity and gene flow as key indicators of evolutionary potential, we offer guidance on several additional attributes (and their proxies) that may also guide decision-making, particularly in the absence of genetic data. Finally, we outline existing decision-making frameworks that can help managers compare alternative strategies for supporting evolutionary potential, with the goal of increasing the effective use of evolutionary information, particularly for species of conservation concern. We caution, however, that arguing over nuance can generate confusion; instead, dedicating increased focus on a decision-relevant evidence base may better lend itself to climate adaptation actions.

KEYWORDS
climate change, evolutionary adaptive capacity, genomics, knowledge exchange, natural resource management, policy, practitioner, researcher, threatened species

1 | INTRODUCTION

Species today face myriad anthropogenic stressors, all of which can be exacerbated by contemporary climate change. These layered selection pressures (i.e., forces favoring sets of new trait values) are rapidly favoring values falling outside the existing tolerance ranges of many species (Wiens, 2016). Nevertheless, some species exhibit rapid responses to stressors that demonstrate their adaptive capacity, while others fail to respond. Adaptive capacity is the intrinsic ability of a species to adjust to or cope with environmental change (Nicotra et al., 2015). It can include shifts in distribution and phenology, phenotypic plasticity, physiological acclimation, and microevolutionary adaptation (Scheffers et al., 2016).

A key component of species' adaptive capacity to climate change is evolutionary potential (Beever et al., 2016; Thurman et al., 2020). Evolutionary potential (or in the language of climate change vulnerability and adaptation, “evolutionary adaptive capacity”) is the ability of populations to evolve genetically based changes in traits in response to environmental change (Steeves et al., 2017). Evolutionary potential is determined by genetic variation in traits that contribute to the long-term persistence of species in the face of climatic change; a species or population with low evolutionary potential may be more vulnerable to climate change. Although traits are the focus of selection pressures arising from climate change, the term evolutionary potential is often used more generally when: (1) the traits that are adaptive or are represented in a population are unknown or (2) there is uncertainty regarding how the environment may change and which traits are likely to become adaptive.

Genetic diversity may represent a form of resilience (e.g., Ehlers et al., 2008; Plaisted et al., 2020) that reflects evolutionary potential, and, hence, conservation of genetic diversity is increasingly recognized as an important practice for ensuring biodiversity can adapt and persist under current and future environmental conditions (Milot et al., 2020). For instance, genetic diversity has been a focus of international agreements on global biodiversity, such as the United Nations Convention on Biological Diversity's (CBD) Aichi Targets (Target 13) and the Sustainable Development Goals (SDG 2.5; Hoban et al., 2020). However, practitioners still rarely consider evolutionary potential in conservation decision-making (Cook & Sgrò, 2017) and, thus, estimates of genetic diversity are rarely provided in National Reports to the CBD (Hoban et al., 2021). This may be because application of relevant research requires a bridge between the disciplines of conservation practice and evolutionary biology, as well as translation of key evolutionary principles and scientific evidence into decision-relevant insights (Cook et al., 2021). Most management decisions utilizing evolutionary principles (e.g., captive breeding) have been implemented in response to imminent threats, often as a last resort for minimizing the risk of extinction (Hellmann & Pfrender, 2011; Weeks et al., 2016). In contrast, efforts utilizing a forward-looking strategy, for example to increase or facilitate evolutionary potential (e.g., selection for species and genotypes with wide moisture and temperature tolerances; Thurman et al., 2022) are uncommon and are challenged by numerous constraints that have limited the development of appropriate guidance for natural-resource managers (Cook et al., 2021).

Limited application of evolutionary science may partially reflect managers' lack of time and resources (Cook & Sgrò, 2019). However, the lack of site-specific, practical, and defensible strategies based on a diverse body of research addressing different species, ecosystems, and focal questions may play a much larger role. The limited evidence base to inform best-practice evolutionary management of natural systems has led to uncertainty about how to optimally facilitate (or infuse) thinking about evolutionary processes into decision-making (Cook et al., 2021). For example, in many instances, prioritizing genetic uniqueness could increase the risk of extinction (e.g., Weeks et al., 2016). However, uncertainty about the evolutionary consequences of management decisions can lead to paralysis and inaction (Cook & Sgrò, 2019). Moreover, a dearth of real-world examples to enable practitioners to predict the outcomes of evolutionarily based management practices is exacerbated by evolutionary biologists' concerns that recommendations could be taken out of context, ultimately resulting in a lack of clear guidance for practitioners. Finally, it is important that the information provided is aligned with agency decisions being made, protocols, and timelines so that actions can be planned and implemented more effectively (Beier et al., 2017).

Here, we present the outcomes of a multiyear dialog carried out among evolutionary and conservation biologists, molecular ecologists, and natural-resource practitioners, wherein management-oriented participants were asked to articulate general questions about how to manage for evolutionary potential (see Supporting Information S1 and S2). We synthesized practitioners' questions into three common themes: (1) recognizing when action may be necessary because a species is either unable to evolve or evolve at a rate that limits its ability to persist in place; (2) understanding the feasibility of assessing whether a population has high evolutionary potential; and (3) identifying best management practices for facilitating evolutionary potential, including implications for mixing populations. Although our primary focus is on climate change, we acknowledge that innumerable conservation challenges often complement climate-change pressures and can sometimes be the dominant ecological stressors that species or populations face (Díaz et al., 2019). In the following sections, we outline key knowledge needs of practitioners, the available evidence that can address them, and remaining challenges to incorporating information on evolutionary potential into natural-resource management. Our intent is to inform management of evolutionary potential across a range of management targets, including populations, ecotypes, and subspecies/species. We suggest that consistent dialog, improved methods for knowledge exchange, and, ideally, coproduction are required to support optimal considerations of evolutionary potential that lead to better conservation outcomes.

2 | RECOGNIZING WHEN TO ACT

In this section, we highlight focal questions related to evolvability and how to recognize it. Specifically, we provide the available evidence in the context of species vulnerability, as a core component of management and adaptation planning under climate change.

2.1 | Can evolutionary rates keep pace with contemporary environmental change?

The evidence regarding whether a species' rate of niche evolution can keep pace with the rate of contemporary environmental change is unclear (Merilä & Hoffmann, 2016), but such rates assuredly vary among species. Most research on this topic has been theoretical or conducted using model systems, comparing evolutionary rates based on historical conditions to future climate- or land use-change scenarios (Merilä & Hoffmann, 2016). For example, Quintero and Wiens (2013) used climate data along with phylogenies of tetrapod species to compare estimates of past rates of niche evolution with the projected rate of future climate change. Across 17 animal clades, rates of niche evolution in the paleorecord were 10,000–100,000 times slower than the projected pace of climate change from now through 2100 (Quintero & Wiens, 2013). Consequently, necessary rates of climate-niche evolution have the potential to be unprecedented under projected climate change, which could lead to many extirpations (Hellmann & Pineda-Krch, 2007; Merilä & Hoffmann, 2016; Quintero & Wiens, 2013; Wiens, 2016).

A weakness of theoretical studies includes the assumption that historical rates of evolution were constant over time. Instead, the pace of evolution could have varied, causing models to under- or over-estimate historical rates of change. Moreover, selection pressures may be much greater under contemporary climate change, potentially resulting in faster rates of evolution in at least some taxa. There are some encouraging examples where species' evolutionary responses have matched the velocity of contemporary climate change, including in fish (Kovach et al., 2012), birds (Karell et al., 2011), plants (Franks et al., 2014), and insects (Brakefield & de Jong, 2011).

2.2 | What are the characteristics of species with greater evolutionary potential?

Several key species attributes or ecological characteristics (Table 1) can be used to determine when species are more likely to evolve to accommodate changes in climatic (or other environmental) conditions. The importance of *genetic diversity* and *gene flow* for evolutionary potential is well understood; higher levels of overall genetic diversity increase the likelihood of population and species persistence (Kardos et al., 2021; Ørsted et al., 2019; Weeks et al., 2017; Willi et al., 2022). For example, a suite of indicators for monitoring genetic diversity that are relevant for a broad range of wild species have been proposed for post-2020 CBD (Hoban et al., 2020). Moreover, genetic diversity, differentiation, and inbreeding metrics, were proposed as potential Essential Biodiversity Variables (EBVs) to be considered by the Group on Earth Observations Biodiversity Observation Network (GEO BON; Hoban et al., 2022). The utility of indicators of genetic diversity for understanding evolutionary dynamics can be dependent on the type and range of genetic markers evaluated, number and location of populations sampled, and the appropriate method of analysis (see section on when to use molecular tools, below).

Phenotypic variation is important because the phenotype (i.e., the outward expression of the genotype) directly interacts with the environment and responds to natural selection (Hendry et al., 2011). Consequently, greater phenotypic variation can suggest a population is already evolving. Outwardly visible phenotypic variation, such as certain morphological (e.g., color, size) or behavioral characteristics (e.g., phenology, habitat use), may be more easily assessed than biochemical or physiological traits. For example, phenological variation in the timing of spring growth onset in alpine plants has been shown to be tightly linked with snowmelt and air temperature (as opposed to photoperiod) in the Swiss Alps (Vitasse et al., 2017); these phenological shifts are often favored at range edges (warm and cold) and can be associated with tradeoffs, such as damage from increased exposure to frost events (Willi & Van Buskirk, 2022). Furthermore, snowshoe hares (*Lepus americanus*) in the Rocky Mountains, which are white in the winter and brown in the summer, are increasingly mismatched with their environments (i.e., white hares in brown, snowless backgrounds) because of shorter winters associated with contemporary climate change, making them more susceptible to predation (Mills et al., 2013). Hares that stay brown all winter are found farther west in areas where prolonged snow cover is uncommon, and researchers are exploring the potential for adaptive capacity in coat color in regions where the genotype–environment mismatch makes populations increasingly less fit (Jones et al., 2020).

Population size can be positively associated with genetic diversity (Frankham, 1996; Willi et al., 2022) and can be used as a proxy for evolutionary potential (Thurman et al., 2020) if past population sizes are known. For instance, past bottlenecks, recolonizations, and founder events can reduce genetic diversity and evolutionary potential (Frankham, 1996), even in larger populations. Effective population size (N_e; the number of individuals actively reproducing in a population) is directly related to genetic diversity. Effective population size reflects population history and a species' mating system or fecundity and can be used to infer future genetic diversity (Hoban et al., 2022). A rule of thumb that an N_e of 500–1000 individuals may be enough to maintain evolutionary potential is useful when estimates of N_e are available (Frankham et al., 2014; Jamieson & Allendorf, 2012). Alternatively, a target adult census size (N_c) of 5000 can be an appropriate replacement, where N_e/N_c ratios are assumed to be approximately 0.1 (Frankham, 2021).

Life-history characteristics, such as generation time, life span, body size, and mating system, are often associated with evolutionary potential, as well as the capacity to respond to changes in different aspects of climate change (e.g., decreasing snowpack, increasing aridity; Haaland & Botero, 2019). In general, longer generation times, and, thus, fewer opportunities for beneficial adaptations to arise, are associated with species that have larger body sizes and longer lifespans. Furthermore, species with more promiscuous or fecund life-history strategies will likely retain greater levels of genetic variation than those with slower reproductive rates (Thurman et al., 2020).

Variation in fitness components, such as survival, reproduction, or mating success, could indicate genetic variance in fitness and that a population has evolutionary potential. This genetic variance can manifest as varying vital rates (e.g., birth and death rates) wherein only a portion of individuals in a population possess traits that can tolerate changing environments and those that do not are

TABLE 1 Representative attributes and ecological proxies that can be used to assess evolutionary potential, including their applications and context dependencies (or limitations) and example management applications

Attributes associated with evolutionary potential	Proxies	Context-dependencies or caveats or cautions	Examples of hypothetical management applications
Genetic diversity (GD)	Population size across time; geographic-range size; niche breadth or ecological specialization; location within the range relative to an ecological gradient	Requires molecular tools; some populations purged of deleterious alleles may have low genetic diversity but still be viable; neutral diversity (based on genes that are not selected upon) may not always be indicative of adaptive diversity (based on genes that are under selection)	Improve or maintain habitat quality and connectivity; expand suitable ecological space for population(s); assess the need for, and risk of, mixing populations
Gene flow	Habitat connectivity; geographic distance between populations; movement studies of marked animals	Gene flow that is too high can decrease local adaptation; gene flow that is too low can decrease genetic diversity and potentially rates of adaptation. The spatial structure of connections among geographically separate populations affects the extent to which gene flow supports adaptive potential rather than only countering genetic drift, and so on (Lenormand, 2002)	Increase connectivity among populations through corridor management; deliberate translocations to increase gene flow among disconnected populations
Phenotypic variation	Geographic-range size; niche breadth or ecological specialization; location within the range; functional trait diversity	It is easy to measure for external traits, such as body mass and leaf area, but difficult to assess when phenotypes are not outwardly visible	Translocate individuals with phenotypes that are adapted to current and future environments
Population size (or effective population size) assessed genetically (*linked to genetic diversity*)	Range/distribution size; niche breadth or ecological specialization; location within the range; population-size estimates through time	Need many genetic samples to achieve a good estimate; knowledge of demographic history (population reductions, recolonizations, founder events) is needed to link census size to genetic diversity	Same as for genetic diversity (improve habitat quality and connectivity, etc.)
Fitness components (survival, fecundity and other measures of reproductive output)	Changes in population size; changes in age structure within populations; reestablishment of reproductive events (e.g., flowering, seed set)	Vital rates can vary because of natural climate variability and correlative selection - identifying natural selection as the causal factor is difficult without experimentation (*may need longitudinal research*)	Manage nonclimate-related threats, such as habitat quality, invasive species, and disease, to maximize population size. Manage a diversity of habitats that vary in climate exposure to increase the likelihood that some populations respond effectively under natural selection
Life-history characteristics (generation time; reproductive strategy; life span; mating system)	Body size; trophic level; local abundance across time; recruitment	Some characteristics such as life stages that are in diapause/dormancy or in cryptic locations (e.g., soil) can be difficult to assess; requires longitudinal studies, given that characteristics can vary across generations (independent of the selective force)	Prioritize assessment of species possessing life-history characteristics that are likely to have lower evolutionary potential

BOX 1 Use of proxies to assess evolutionary potential of the rusty-patched bumble bee (*Bombus affinis*)

Historically, the rusty-patched bumble bee (*Bombus affinis*) was broadly distributed across prairies and grassland habitats in the eastern and upper-Midwest portions of Canada and the USA (USFWS, 2016). The species experienced a widespread and steep decline in the early 2000s, precipitating its endangered status in 2010 in Canada (per COSEWIC) and in 2017 in the United States (per the Endangered Species Act of 1973). Today, the species is extant in 11 states (USFWS: Rusty-Patched Bumble Bee Map, accessed October 2021) and 1 Canadian Province (ECCC, 2016), a >50% reduction in its native range. The exact cause of the decline is unknown, but evidence suggests a synergistic interaction between an introduced pathogen and exposure to pesticides (USFWS, 2016). The remaining populations are exposed to a myriad of interacting stressors, including other pathogens, pesticides, habitat loss and degradation, nonnative and managed bees, the effects of climate change, and small-population dynamics (USFWS, 2016).

As part of a Species Status Assessment leading up to its U.S. listing under the Endangered Species Act, USFWS scientists wanted to assess changes in the species' adaptive diversity but limited genetic data were available. Therefore, ecoregions were used to delineate unique areas of adaptive diversity across the species' range, as the boundaries of these ecoregions are differentiated based on precipitation levels and temperature (important determinants of *B. affinis* survival and reproductive success). Using past, current, and future projections of *B. affinis* occurrences, change in adaptive diversity over time was estimated. Key assumptions in the assessment were that the ecoregions accurately captured the full spectrum of *B. affinis* adaptive diversity and that an ecoregion-wide extirpation would signify a loss in adaptive diversity. This work allowed scientists to incorporate the species' evolutionary potential in their assessment of the species' current and future viability. Building off this work, the U.S. recovery plan refined the ecoregion units and specified restoring and maintaining populations in each unit as a recovery criterion, with the intent of preserving the species' adaptive diversity and thereby maintaining the species' ability to adapt to changing environmental conditions (USFWS, 2021).

lost to the process of natural selection. Generally, fitness components (or vital rates) that are important contributors to population growth for a particular species will have low variation in environments they are already adapted to (i.e., the demographic buffering hypothesis; Pfister, 1998). However, detecting this type of variance in practice is challenging, as it requires that vital rates have been consistently measured over time. Comparative studies of different populations that capture a snapshot in time (i.e., space-for-time substitutions) may be less likely to observe fractions of populations that failed to adapt (presumably contributing to greater variation) and were lost to the process of selection (Merilä, 2012).

Ecological characteristics may also be used to infer evolutionary potential (Box 1). For instance, species with *broad geographic distributions* (particularly those encompassing broad environmental variability) or *ecological niches* are more likely to have higher genetic diversity and adaptive capacity (Nicotra et al., 2015). An ability to use a broad array of resources, both in space and time, can buffer populations from unfavorable conditions. Conversely, species with narrow distributions (e.g., endemics), or that use a limited range of resources (i.e., ecological specialists), likely have limited capacity to cope with changing environments or variable disturbance regimes (Li et al., 2014). A potential caveat associated with this generality is when a species comprises multiple disjunct and isolated populations despite a large geographic distribution; genetic diversity can erode through genetic drift similarly to a species with a small geographic-range size. Loss of geographic range extent may also be used as a comparative tool to assess evolutionary potential among many species (e.g., see Box 1 of Mimura et al., 2017); such analytical approaches can provide insights regarding which species may be most in need of management attention.

Location within the range can also be a relevant indicator of adaptive potential. The Abundant-Centre Hypothesis posits that species' abundance and performance decrease toward the range periphery (e.g., northern or southern latitudinal extent) due to a deterioration of climatic conditions relative to the species' niche, and that peripheral populations can have lower genetic diversity and N_e, and higher genetic differentiation due to population isolation (Eckert et al., 2008). However, species' distributions within ranges, and degree of climate-change exposure are often complex and vary in response to topographic patterns and other factors that influence microclimates, and scale of measurement (Billman et al., 2021). Some species have healthy peripheral populations yet have core populations that are less healthy because of factors like poor quality habitat (Brown, 1984) that can occur in any portion of the range. Furthermore, local adaptations of peripheral populations may inhibit adjustment to new environments, as has been shown in butterflies (O'Neil et al., 2014; Pelini et al., 2009). Supporting natural or historical patterns of connectivity and gene flow across a species' range can increase adaptive potential in response to environmental change.

3 | FEASIBILITY OF MEASURING EVOLUTIONARY POTENTIAL

Measuring evolutionary potential can be extremely valuable for informing management under climate change but can be difficult to quantify, particularly because multiple mechanisms can be responsible for observed phenotypic changes. In particular, phenotypic plasticity and epigenetic changes can be challenging to distinguish from evolutionary (genetic) adaptation in the absence of common garden experiments (Hoffmann, Weeks, & Sgrò, 2021; McGuigan et al., 2021) because they can all result in phenotypic changes in response to environmental triggers or stressors. At the same time, phenotypic plasticity can also be considered a trait in itself that has the potential to evolve. It can be an important mechanism for responding to climate change (Beever et al., 2017), particularly for long-lived species (e.g., Cooper et al., 2019).

Molecular tools can provide valuable insights into species' evolutionary, plastic, or epigenetic changes (McGuigan et al., 2021). Several types of experimentation can also be used to infer evolutionary potential when there is prior knowledge of the population of interest (e.g., pedigree data) or ability to control for key environmental factors (Merilä & Hendry, 2014). However, in the absence of the data required to assess and distinguish these evolutionary processes, proxies like population size or demographic history, are often used as indirect measures when their caveats are well understood. The following sections describe the strengths and weaknesses of using each of these approaches.

3.1 | When can molecular tools be helpful?

Molecular tools for assessing genetic variability and change are useful when precise estimates of genetic diversity are needed to inform targeted management strategies. Although their broad-scale use is likely to be limited due to cost, these costs are rapidly decreasing, and the tools can be applied to many types of questions. Examples of use include determining inbreeding rates when inbreeding depression is suspected (e.g., Townsend et al., 2009), assessing effectiveness of genetic restoration efforts (e.g., Weeks et al., 2017), identifying genetic erosion (e.g., Thompson et al., 2019), detecting hybridization (e.g., Garroway et al., 2010), identifying local adaptations (e.g., Peláez et al., 2020), monitoring of genetic diversity (e.g., Hollingsworth et al., 2020), assessing carnivore population size to avoid wildlife-related conflicts (e.g., Åkesson et al., 2022), evaluating ecosystem resilience (e.g., Wernberg et al., 2018), or acquiring baseline information about genetic diversity for conservation-planning purposes (e.g., Lorenzana et al., 2020). Moreover, molecular tools can be combined with spatial data to identify factors that are governing genetic structure and connectivity (i.e., landscape genetics) and help practitioners identify which populations are most critical to maintaining or restoring gene flow across a network or metapopulation (Castillo et al., 2016), although care must be taken to ensure appropriate sampling and analyses (Hoffmann, Miller, & Weeks, 2021). Finally, experimental association studies can be used to identify associations between certain regulating genes and traits. Regulating genes can be "turned on" (i.e., expressed) under certain environmental conditions and affect traits like leaf area and plant height, as has been shown in populations of the common sugarbush (*Protea repens*) in response to experimental drought in South Africa (Akman et al., 2021).

TABLE 2 Examples of the types of evolutionary questions that can be answered using metrics of adaptive vs. neutral genetic diversity

Evolutionary topics/questions	Neutral genetic diversity	Adaptive genetic diversity
Questions relating to the need for management action		
What is the level of genetic diversity in a population?	X	
Is inbreeding occurring?	X	
Is inbreeding depression occurring?[a]	X	
Is genetic drift occurring?	X	
Is hybridization occurring?	X	
How has the population size changed historically?	X	
Questions to support the design of potential management actions		
Is there genetic differentiation among populations?	X	
Is there evidence for genetic variation along environmental gradients?	X	X
Is there evidence of past adaptive introgression into a population?		X
Questions relating to the success of management action		
Was genetic diversity in the population increased?	X	
Was evolutionary potential increased?		X
How much dispersal is occurring within and across populations?	X	

[a] Requires measures of fitness or fitness components to fully assess.

The choice of genetic markers used for estimating genetic diversity depends largely on the management question (Table 2). Mitochondrial DNA is useful for exploring biogeographic and phylogenetic questions because its maternal mode of inheritance and lack of recombination provides insights on parentage (Hartl & Clark, 1997). Consequently, the marker is often used for distinguishing among evolutionary lineages, resolving taxonomies, or identifying interspecific hybridization (see section below on when to mix populations). Many measures of genetic diversity use nuclear DNA, which can evolve rapidly in some regions of the genome and is able to capture more recent responses to land-use or environmental change (e.g., Thompson et al., 2019). These genetic diversity estimates fall into two general categories: those based on genes that affect fitness or are under selection (i.e., adaptive diversity) and those that are unlikely to affect fitness or are not selected upon (i.e., neutral diversity; Holderegger et al., 2006; Hoffmann et al., 2015). Nuclear DNA markers like microsatellites can be useful to inform questions, such as the level of inbreeding or hybridization (Table 2). Questions related to local adaptation can be assessed using nuclear genetic markers found across both neutral and adaptive portions of the genome, such as single nucleotide polymorphisms (SNPs). SNPs have become the marker of choice because they are easier to collect than microsatellites, and the mutational process that generates them can be more easily captured in statistical models used to distinguish between evolutionary processes. This means that SNPs can be used to make inferences about gene flow, drift, demography, and phylogeny, in addition to testing for signals of selection and adaptation along environmental gradients. Given that thousands of SNPs are typically scored, they provide more precise estimates of population processes such as migration than other markers, especially when rates of gene flow are low (Hoffmann et al., 2015).

If the aim is to link genomic variation to functional variation (i.e., an understanding of the function for each gene; Hendry et al., 2011; Hoffmann et al., 2015; Hoffmann, Weeks, & Sgrò, 2021) to fully assess how a particular change in allele frequencies may affect evolutionary potential (Box 2), an annotated reference genome (i.e., a nucleic acid sequence assembled into a representative set of genes for a particular organism of a species) is needed. A reference genome of a closely related species can be used when one for the target species is either not available or has gaps (e.g., use of a domestic sheep [*Ovis aries*] reference genome for bighorn sheep [*Ovis canadensis*] assessments of evolutionary potential; Buchalski et al., 2018) but slight differences can confound results.

Although molecular approaches are increasingly accessible through access to commercial sequencing platforms, high-level skills in bioinformatics are needed to ensure the quality of the data being used. Specialist training and collaboration with molecular ecologists can help to support the appropriate choice of statistical models used in analyses (Hoffmann, Weeks, & Sgrò, 2021). Methodological and analytical limitations of using SNPs to infer selection and local adaptation must be carefully considered (Hoffmann et al., 2015; Hoffmann, Weeks, & Sgrò, 2021). In particular, inferences about selection and adaptation from genomic studies of SNP data along environmental gradients must account for the high rate of false positives resulting in misleading conclusions about adaptation. A thorough understanding of evolutionary processes is necessary to ensure that data are analyzed, and results interpreted appropriately. Although considerable work is being carried out to make genomic data available in a format useful for decision making (e.g., Threatened Species Initiative; Hogg et al., 2022), we still see genuine collaborations (wherein stakeholders are

BOX 2 Use of molecular tools for exploring evolutionary potential of gray box (*Eucalyptus microcarpa*)

The gray box (*Eucalyptus microcarpa*) is native to southeastern Australia. The once-widespread Grey Box Grassy Woodland community has been extensively cleared and is now a nationally threatened ecological community (DSEWPC, 2012). This vegetation community is home to numerous plants, birds, insects, and mammals, but only 10%–15% of the historical range remains. Extensive clearing for agriculture has left a legacy of small fragments of gray-box woodland scattered across its previous distribution, prompting widespread use of this species in restoration projects.

Recent work sought to inform restoration efforts by exploring the evolutionary potential of gray box under projected climate change. Researchers from the University of Melbourne and CSIRO collected DNA from 20–30 individual trees across 26 remnant populations spanning temperature and precipitation gradients across New South Wales and Victoria (Jordan et al., 2017). Greater than 4200 SNPs were identified, and 81 of those were found to potentially be under selection from climatic variables, including measures of temperature, aridity, and precipitation. The authors used an annotated reference genome for a closely related species used in forestry (*E. grandis*) to infer the function of a small portion of putatively adaptive SNPs potentially related to growth, development, and stress responses, all processes likely to be affected by climate. However, these adaptive genes occurred randomly across chromosomes, suggesting that each has a small effect on local adaptations (i.e., the phenotype is determined polygenically).

This work is consistent with many other genomic investigations, in that adaptive traits are often controlled by many genes (each with small effect), but that there can be much standing genetic diversity to work with across the distribution of some wild populations. However, given the large number of genes under selection, it may be difficult to determine whether their optimal frequencies can keep pace with projected climate change, especially if populations are fragmented. Consequently, management of northern gray box populations, particularly in locations where current climate conditions are closer to those expected under climate change, may offer the potential to use climate-adjusted provenancing strategies to support restoration of southern populations (Prober et al., 2015).

involved at an early stage) between practitioners and evolutionary biologists as essential.

Despite these challenges, molecular tools are increasingly being used to estimate genetic diversity in conservation assessments, and molecular ecologists and evolutionary biologists are often sought after for assistance with answering management-relevant questions. Stronger partnerships (i.e., genuine collaborations) between researchers and practitioners will strengthen the decision-relevance of molecular work, and help practitioners gain critical experience in investigating and applying information on evolutionary potential. As management agencies hire molecular expertise as part of their organization (e.g., U.S. Fish and Wildlife Service, Branch of Species Status Assessment Science Support; California Department of Fish and Wildlife, USA) to accommodate the growing interest in, and applications of, genetic information, and costs continue to decline, we expect practical examples and guidance on highest-priority applications to increase. On-going collaborations with evolutionary biologists will be pivotal to the success of such endeavors. However, costs will likely still be prohibitive for some agencies or there may be existing decision deadlines that cannot wait for better information to become available, so continued work to understand when microsatellites, which can sometimes be cheaper or more widely used than SNPs, provide sufficient information will be helpful to support effective decision-making.

3.2 | What other approaches can be used to determine evolutionary potential?

Common-garden, animal-model, or experimental-evolution investigations can indicate whether a species may be able to adapt to climate change. For example, Frank et al. (2017) used a common garden approach to measure fitness of European trees under projected climate change; whereas European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*) were found to be potentially maladapted to future conditions based on a suite of measured growth and phenological traits, silver fir (*Abies alba*) may be less vulnerable to changes (Frank et al., 2017). Advantages of using experimental studies include potentially being able to differentiate between alternative causes of phenotypic change. Teplitsky et al. (2008) used an animal-model study to determine whether body size of red-billed gulls (*Chroicocephalus scopulinus*) decreases with increasing temperatures, as would be expected under Bergmann's Rule (Bergmann, 1847). The authors found that, although body size did decrease, it was most likely due to phenotypic plasticity rather than evolutionary change (Teplitsky et al., 2008).

In practice, carrying out such experimental studies on natural populations can be problematic because they sometimes require large amounts of preexisting data, the ability to control for certain environmental factors, or are limited to species with specific life history traits. For example, experimental-evolution investigations are generally best carried out on species with short generation times to allow for observations of evolutionary responses to controlled environmental conditions. Additionally, animal model studies require pedigree data, which are not available for most natural populations. Despite some of these challenges, experimental studies can be a powerful approach for understanding evolutionary potential when time, data, and expertise are available. Merilä and Hendry (2014) provide an overview of multiple approaches that can be used for determining genetic and plastic changes, as well as their advantages and disadvantages.

3.3 | When is it appropriate to use proxies and rules of thumb?

Proxies or rules of thumb can be used for assessing evolutionary potential if potential caveats are accounted for (Table 1). For example, inferring evolutionary potential from a life-history trait like reproductive strategy may be misleading and inappropriate if the population of interest recently experienced a bottleneck, causing genetic diversity to be much lower than what would be expected for species with high reproductive output. Otherwise, the decision to use proxies or rules of thumb largely reflects the management realities of needing a feasible, timely, low-cost approach. Collecting new data to inform evolutionary assessments may not be feasible, and practitioners may already be collecting or have access to data that can indirectly inform assessment of evolutionary potential (e.g., species distribution models that consider the potential for intraspecific variation; Hällfors et al., 2016; Smith et al., 2019). Furthermore, use of ecological proxies (e.g., habitat connectivity) may be more feasible for situations where species (or multiple species) occur in remote areas or across large scales (that span more than one jurisdiction) and are difficult to sample. However, in some cases, collection of proxy data may be no less expensive than molecular studies. For example, large-mammal management often uses DNA collected from noninvasive genetic sampling to generate a database of unique individuals (via genetic tags) that are used to estimate population size using open- and closed-population models in software like MARK (White & Burnham, 1999). These same databases of individual genotypes could also be used to estimate genetic diversity. Because costs of DNA analysis have dropped considerably in recent decades, practitioners may find "genetic tagging" more cost-effective than capture and handling methods (Lamb et al., 2019).

The choice of proxies or whether to use proxies in place of molecular methods can also depend on the level of risk. For example, more may be at stake when making management decisions for protected species or those of high conservation concern. Certain proxies have a greater amount of research connecting them with genetic diversity (e.g., Ne; Jamieson & Allendorf, 2012) and may be considered more reliable. Hoban et al. (2020) reviewed the strengths and weaknesses of a list of potential genetic indicators released by the CBD. Three indicators were identified as being S.M.A.R.T. (i.e., Specific, Measurable, Achievable, Relevant, and Time-bound), including effective population size (N_e), the number of remaining populations, and the number of species or populations already being monitored using DNA-based methods (Hoban et al., 2021). Although proxies may be an obvious choice in many situations, practitioners may prefer a more direct measure of evolutionary potential, especially if they have access to available expertise and resources needed to calculate measures of genetic diversity.

4 | BEST MANAGEMENT PRACTICES FOR FACILITATING EVOLUTIONARY POTENTIAL

Diverse management strategies have been used to help species better cope with the effects of climate change (LeDee et al., 2021), and many others have been proposed (Thurman et al., 2022). As natural-resource practitioners become increasingly accustomed to identifying and implementing these management strategies, concerns have increased regarding best practices for promoting evolutionary potential or favorable traits. Determining where in a species' range management should focus, when to implement high-risk actions, and the potential for unintended consequences were topics of particular concern that were voiced.

4.1 | Where in a species' range should management focus?

In the absence of information regarding potential local adaptations and beneficial traits, being strategic about where to focus management of evolutionary potential may increase the likelihood of success, despite limited resources. Most extirpations have occurred at the *trailing edge of a species' range* (Freeman et al., 2018), and establishment of new populations along the *leading edge* has not kept pace for many populations (Wiens, 2016). Actions targeted at trailing-edge populations when they can be identified can include efforts such as genetic restoration and rescue (Bell et al., 2019). These reactive efforts are intended to increase genetic diversity in inbred populations and minimize loss of fitness associated with inbreeding. However, reintroductions of climate-sensitive species to locations where past extirpations have occurred because of deterministic changes in climate (i.e., where climate may no longer be suitable or will become unsuitable soon) may be less successful than reintroductions to locations that have experienced nonclimatic catastrophes (e.g., see Box 1 of Beever et al., 2016). Leading-edge populations are frequently the target of more-novel actions (Thurman et al., 2022), such as receiving nonlocal provenances (e.g., genotypes, seeds, individuals) to facilitate adaptation by endowing the recipient population with potentially adaptive alleles or gene variants. Leading-edge actions are considered more proactive because they anticipate potential changes to distributions and fitness associated with novel conditions.

Evolutionary potential can also be explicitly managed when restoring *disturbed* or *degraded landscapes*. Specifically, seed material for restoration can be selected to maximize genetic diversity (Byrne et al., 2011; Sgrò et al., 2011). In particular, local-provenance seed can be mixed with some proportion of seed from genetically diverse populations that inhabit climatically diverse regions (Prober et al., 2015). This can preemptively increase adaptive capacity and evolutionary potential under future climatic conditions.

Ensuring connectivity across *environmental gradients* is important for supporting large populations, allowing for migration, and maximizing opportunities for unassisted evolutionary adaptation to a broader array of potential future conditions by, for example, capturing evolutionary hotspots within a species' range (Sgrò et al., 2011; Weeks et al., 2011). This, in turn, allows for the persistence of locally adapted populations, adaptive genetic diversity, and evolutionary potential. Efforts to ensure a gradient of environmental conditions are protected can also maximize opportunities for persistence at the species level, particularly if future conditions (or species response to future conditions) are uncertain (Anderson & Ferree, 2010). Building on this idea, The Nature Conservancy's "Resilient and Connected Network" emphasizes protection of terrestrial sites that have higher-than-average topographic complexity for a given geology or soil type, with the idea that these examples capture the widest possible variety of microsite conditions, which is used as a proxy for higher species and genetic diversity (Anderson et al., 2014; https://maps.tnc.org/resilientland/). Management of gradients across landscapes has been applied to protected-area planning, with most recent work emphasizing the intention of facilitating species' future range shifts (Littlefield et al., 2017).

4.2 | Can well-intended management actions do harm? What are no-regrets practices that usually support evolutionary potential?

There are many examples of management actions that have led to unintended negative consequences. Although most actions used to promote evolutionary potential can involve risk, some may be riskier than others (e.g., hybridization). A well-known example of negative consequences is the introduction of ibex populations from Turkey (*Capra hircus aegagrus*) and the Sinai Peninsula (*Capra nubiana*) to a population in the Tatra Mountains in Slovakia (*Capra ibex*), which produced hybrids that bred too early and caused the entire population to collapse (Templeton, 1986). However, many decision frameworks are now available that can help practitioners avoid such catastrophes. For example, Frankham et al. (2011) provided a decision tree for determining the probability of outbreeding depression when mixing two populations. The authors suggested that risk is increased when two populations exhibit at least one of the following criteria: (1) fixed chromosomal differences (which can be determined using molecular tools), (2) are distinct species, or (3) have been separated for at least 500 years, or occupy different environments (e.g., alpine vs. low elevation) for >20 generations (Frankham et al., 2011). Thus, even without molecular tools, a practitioner would likely choose against mixing those populations today, given that *C. h. aegagrus* and *C. nubiana* are now considered to be different species and they occupied warm, arid environments and had been separated from *C. ibex* (which occupied cool, high-elevation environments) for hundreds of years. Sometimes actions could be wasteful, for example, if attempts to increase genetic diversity result in genotypes that are not favored in the new environment; this scenario may be particularly problematic in cases where a species is declining and source populations are hard to come by (e.g., see Box 1 of Beever et al., 2016).

The link between genetic variation, evolutionary potential, and population size makes maintaining relatively large and well-connected populations critically important for long-term viability for most species (Forester et al., 2022). Even where large populations do not exist, maintaining connectivity to facilitate gene flow will support evolutionary potential and genetic diversity across populations (Sgrò et al., 2011). Exceptions include the potential for enabling disease transmission and epidemic risk (Hess, 1996). Furthermore, increasing connectivity to areas where local adaptations may be important, such as areas mentioned above (climate refugia at the trailing edge of the geographic range, leading edge of the range, environmental gradients), has the potential to facilitate movement of maladapted individuals to those regions (i.e., gene swamping; Lenormand, 2002). A careful approach is to consider population size and genetic distinctiveness. In small populations, genetic drift can overpower selection and it may be better to supplement them demographically if populations have not been separated for more than 500 years (Ralls et al., 2018) and are from large and genetically diverse populations (Ralls et al., 2020). Furthermore, understanding patterns of rare alleles (e.g., genes that are low in overall frequency) and facilitating their presence through improving habitats may preserve potential adaptations. Finally, recent research has sought to identify regions where management actions may be most useful, with the goal to reduce wasteful actions. For example, Gougherty et al. (2021) showed that genetic rescue via migration of balsam poplar (*Populus balsamifera*) may be least successful along the longitudinal edges of its range because of potential maladaptation to future climate scenarios.

4.3 | When can population mixing be considered?

Intraspecific mixing of populations may be appropriate when populations are small, isolated, and potentially inbred (i.e., genetic rescue; Hoffmann, Miller, & Weeks, 2021) or when populations are stressed because of environmental change (i.e., evolutionary rescue; Hoffmann, Miller, & Weeks, 2021). Furthermore, when fitness to new environments is known, introducing individuals (or their genotypes) to areas where they may be preadapted to current or future conditions (i.e., climate-adjusted provenancing; Prober et al., 2015) is an increasingly common consideration for long-lived species, especially some plants (Hoffmann, Miller, & Weeks, 2021). Recent work has also demonstrated that mixing can have many benefits for evolutionary potential (Zecherle et al., 2021). The use of risk-assessment frameworks is an important consideration to reduce the potential for harm (Table 3). Actively weighing the risks of inbreeding depression versus outbreeding depression can achieve better outcomes (Liddell et al., 2021).

Although mixing populations can improve evolutionary potential within a species, mixing different species (i.e., interspecific hybridization) can increase the risk of outbreeding depression (the reduction in any pre- or postmating aspect of reproductive fitness because of attempted crossing of distinct lines/populations, subspecies or even species, Frankham et al., 2011) and should, therefore, be used cautiously. A potential caveat associated with mixing populations arises when species boundaries are unknown. Consequently, it is important that evolutionary lineages have been clearly established before evaluating potential risks. Intentional hybridization can be a consideration for rapid evolution, particularly when the alternative is a high risk of extinction (Hamilton & Miller, 2016), but hybrid offspring are best evaluated in captivity or controlled experiments to assess fitness to different environments (Weeks et al., 2011; Weeks et al., 2017).

TABLE 3 Examples of existing frameworks and decision-support tools to inform best practices for managing evolutionary potential

Management scenario	Source	Context/decision points described
Provenancing	Breed et al. (2013)	Decision tree for seed selection with considerations of climate-change distribution modeling and genetic/environmental differences among populations
	Harrison et al. (2017)	A framework for identifying candidate seed sources for restoration (Provenancing Using Climate Analogues or PUCA)
	Byrne et al. (2011)[a]	A framework for reducing risk associated with revegetation in degraded landscapes
	Prober et al. (2015)[a]	Climate-adjusted provenancing: a strategy for climate-resilient ecological restoration
Mixing of populations	Frankham et al. (2011)[a]	A framework for assessing risk of outbreeding depression
	Weeks et al. (2011)[a] and Karasov-Olson et al. (2021)[a]	A framework for assessing risk of translocating individuals vs. not acting
	Ralls et al. (2018)[a]	Guidance on restoring gene flow to small, inbred populations
	Hoffmann et al. (2021)[a]	A framework for making management decisions around the implementation of genetic mixing
Choosing best management strategy	Ottewell et al. (2016)[a]	A framework for choosing a management strategy based on genetic differentiation and diversity and inbreeding
	Thompson et al. (2021)	A framework for understanding when to *Resist*, *Accept*, or *Direct* changes to ecosystems, including disruption of evolutionary processes

[a] Indicates open-source publication.

As climate change forces many species to shift in space to track suitable conditions, unintentional hybridization may increase with the reorganization of ecological communities and movement of "climate refugees" across the landscape (Urban, 2020). For example, climate-driven hybridization has been documented between northern and southern flying squirrels (*Glaucomys sabrinus* and *G. volans*, respectively; Garroway et al., 2010), polar and brown bears (*Ursus maritimus* and *U. arctos*, respectively; Pongracz et al., 2017), Canada lynx (*Lynx canadensis*) and bobcat (*Lynx rufus*; Schwartz et al., 2004), and blue- and golden-winged warblers (*Vermivora cyanoptera* and *V. chrysoptera*, respectively; Environment and Climate Change Canada, 2016). It is not yet known what percentage of these hybrids has altered fitness under climate change, but interspecific hybridization can lead to nonviable or infertile offspring. For example, research on hybrids of introduced rainbow trout (*Oncorhynchus mykiss*) and native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) showed reduced reproductive success when only a small proportion of ancestry was mixed (Muhlfeld et al., 2009). Proactive assessment of range shifts and potential species interactions may be necessary for detecting hybrids, as well as monitoring to evaluate fitness of hybrid offspring and their location (e.g., Ryan et al., 2018). Managers will then have a choice of three strategies that seek to *persecute* shifting species and/or hybrid offspring, *protect* the native species, or *ignore* this redistribution of biodiversity (Scheffers & Pecl, 2019).

5 | A PATH FORWARD

Our dialog between conservation practitioners and evolutionary biologists has identified several needs related to research, science translation, and application that can inform future natural-resources management under climate change. These include:

- *Filling scientific knowledge gaps*: Although many advances have occurred for understanding species' evolutionary responses to environmental change, predicting evolutionary potential remains a challenge because long-term data sets across a range of geographic distributions and ecological systems are often required. Furthermore, determining whether evolution will be able to keep pace with the rate of environmental change is currently unknown for many species. Additional molecular and experimental approaches for modeling wild, nonmodel species are needed to increase understanding of: (1) factors that may facilitate or constrain adaptations, and (2) effectiveness of management interventions. Research related to "pre-adapted" individuals that may be able to persist under certain climate conditions, which are known either because of trait expression or the ability to survive in certain environments, is critical for decision making. Given the large number of species that may be affected by climate change, research on generalizing evolutionary potential across congeners with similar biological attributes or that exist in similar environments would be useful for informing natural resource management.

- *Building a decision-relevant evidence base*: Case studies are useful for providing evidence of successful and unsuccessful management actions, but their outcomes are often case-specific and lack generalizations; researchers now recognize that a more-comprehensive evidence base of forward-looking (proactive) versus reactive actions under a wide range of contexts can better demonstrate effectiveness of management in natural populations and increase confidence in decision-making (i.e., Cook et al., 2021). Building the capacity for managers to apply insights from evolutionary biology may require investment in science translation and coproduction, processes which facilitate the development of decision-relevant science, and mutual learning across the research and practitioner communities (Enquist et al., 2017; Hällfors et al., 2016).
- *Assessing evolutionary potential*: Proxies or rules of thumb can indicate evolutionary potential, in place of molecular tools, as long as the caveats are well understood. Working directly with researchers and boundary actors and/or utilizing expert-elicitation methods (e.g., Camac et al., 2021) may help practitioners gain a better understanding of current and future threats and potential evolutionary responses of species of interest.
- *Using decision frameworks*: Decision frameworks have been developed to increase understanding of the potential risks and benefits associated with mixing of populations. The risk of outbreeding depression, for example, occurs along a continuum that increases substantially when mixing evolutionarily distant populations or species (hybridization; Frankham et al., 2011; Weeks et al., 2011; Hoffmann, Miller, & Weeks, 2021), and using decision frameworks may minimize concerns for many management situations. At the same time, researchers recognize that risks of mixing need to be weighed more explicitly in conservation studies and to make clear recommendations that can directly inform decision-making (Liddell et al., 2021).

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ORCID

Laura M. Thompson https://orcid.org/0000-0002-7884-6001
Lindsey L. Thurman https://orcid.org/0000-0003-3142-4909
Erik A. Beever https://orcid.org/0000-0002-9369-486X
Ary A. Hoffmann https://orcid.org/0000-0001-9497-7645
Olivia E. LeDee https://orcid.org/0000-0002-7791-5829
Claudia Mengelt https://orcid.org/0000-0001-7869-5170

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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